CALLIANDRA HAEMATOCEPHALA: HISTORY, MORPHOLOGY, AND TAXONOMY

LORIN I. NEVLING, JR., AND THOMAS S. ELIAS

One of the striking ornamental trees of tropical and subtropical climates is the leguminous powder-puff tree. Since its description more than a century ago it has become a widely distributed ornamental plant. The curious background associated with this species has led to considerable taxonomic and nomenclatural confusion over its correct scientific name. As a result of general interest in the genus Calliandra, particularly in its floral biology, we began a routine re-evaluation of C. haematocephala Hassk, and C. inaequilatera Rusby, the two scientific names commonly associated with the powder-puff tree. Our conclusions differ in several significant respects from those of previous investigators, and we present them in the hope that we have clarified a difficult systematic problem.

One of the most critical problems in equating Calliandra haemato-cephala Hassk. with Calliandra inaequilatera Rusby has been that of geographic distribution. Calliandra haematocephala was described by Hasskarl from material in cultivation at the botanic garden in Java. In Hasskarl's original publication he cited his material as coming from the botanic garden at Calcutta under the name of "Ingae haematoxyli." The origin of the material in Calcutta was reported as unknown. This "species" had not been found in the wild, although it had been widely and

correctly assumed to be a plant of American origin.

The type material of Calliandra inaequilatera was described by Rusby from material collected by Miguel Bang in Bolivia near the town of Guanai. This locality is also spelled Guanay, Huanai, or Huanay and is apparently critical in the resolution of the problem (see Figure 1). Guanai lies between the fork of the Río Tipuani and the Río Mapiri at an altitude of about 700 meters. It was established by the Spanish as a mission and as a place of exile for political prisoners. At the confluence of the Tipuani and Mapiri the river becomes the Río Kaka, which soon joins the larger Río Beni. One of the difficulties in developing evidence for the conclusion that the two names apply to the same plant has been the failure to resolve the geographic disparity between Bolivia and Java.

It seems unlikely that a Bolivian Calliandra would have made its way to Java via Calcutta entirely on its merits as an ornamental shrub by the year 1855 (the date of Hasskarl's publication). We believe that such a "migration" can be explained only through an understanding of the outstanding botanical problem of the times, namely Cinchona. The demand for Cinchona bark was tremendous at the turn of the 19th century, and field botanists of the era were sending an alarm to their respective governments. Exploitation of the bark of the great Cinchona trees was advancing at a much too rapid rate. By 1830 the governments of Britain,

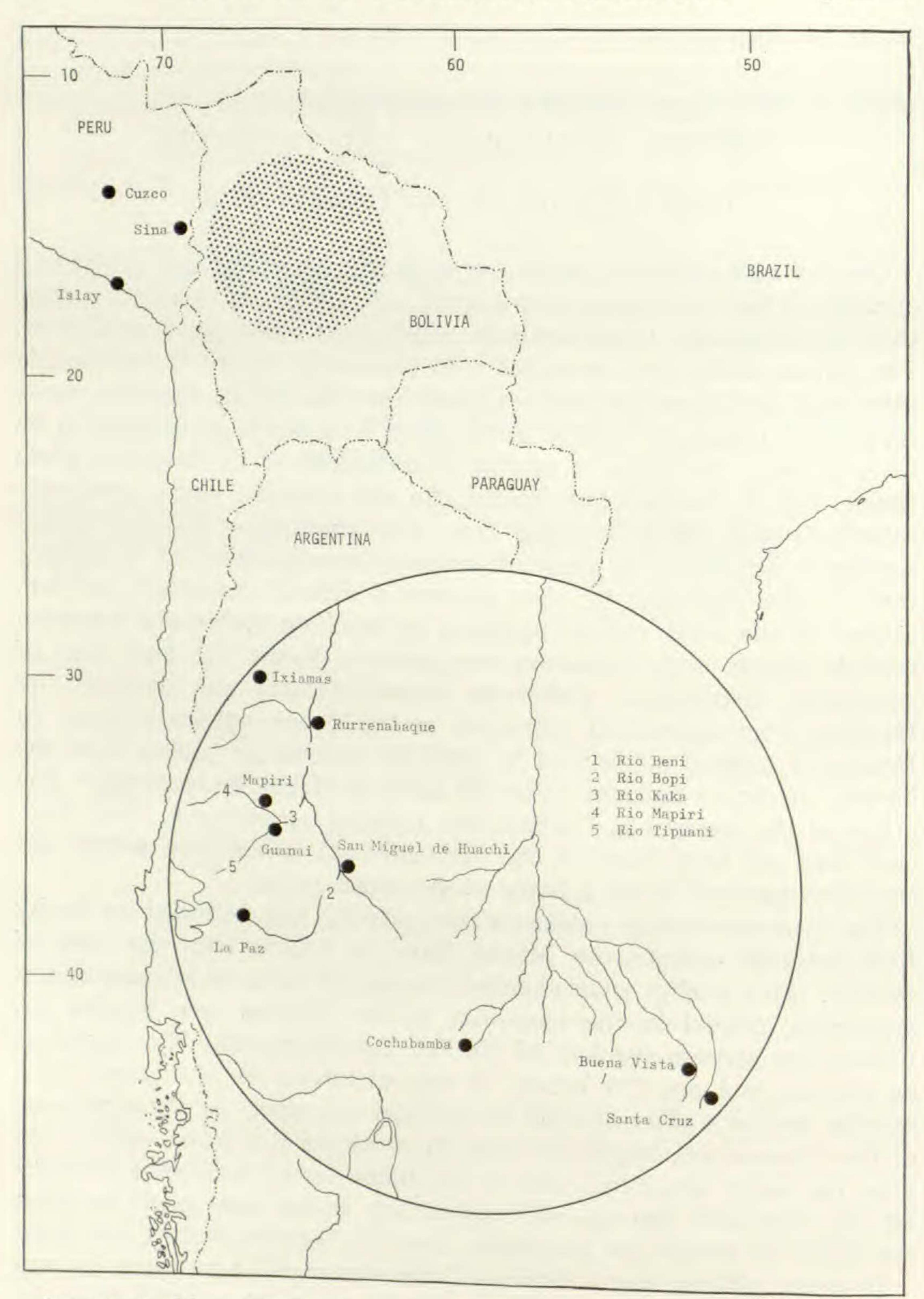


FIGURE 1. Map showing important localities and rivers significant in some historical aspects of Calliandra haematocephala. Inset is enlargement of stippled area.

France, and Holland began to believe the field reports and became concerned that their bark source would be dangerously diminished. Testing for high-yielding bark was underway, but it was relatively ineffective because of lack of understanding of the taxonomy of the group. The goal

was to isolate a species that would yield high percentages of sulphate of quinine. At approximately the same time, the Bolivian government realized the threat to her Cinchona resources, which were a primary source of income from the outside, and began to take repressive steps to prevent the over-exportation of Cinchona bark. In 1845, it granted a five-year monopoly to the Spanish firm of Jorge Tesanos Pinto and Company in return for \$119,000. The agreement limited the amount of bark to be taken. In 1849, by presidential decree, the monopoly was broken because of low wages paid to the bark gatherers (cascarilleros). Several subsequent monopolies were established, but all collapsed in a few years because of financial difficulties. In spite of the series of impending monopolies, or perhaps because of them, the major powers banded together in various attempts to get seeds or seedling plants of Cinchona from various parts of the New World. One of the main objectives was to be Cinchona calisaya Wedd. (= C. officinalis L. fide Standley). This species was known from southern Peru and Bolivia, but the exact limits of its distribution were unknown. Accordingly, in 1843, the Count de Castelnau, the Viscount d'Osery, and Dr. H. A. Weddell entered Bolivia via an overland route through Brazil to collect material of Cinchona and particularly to establish the southern geographical limit of Cinchona calisaya. Through a series of mishaps Dr. Weddell was eventually separated from the other members of the party; the Count returned to Europe, while the Viscount disappeared into the upper Amazonian Basin, never to be seen again. Weddell explored the Bolivian Cinchona forests from Cochabamba through Ayopaya and Enquisivi. In 1847, he entered the province of Caupolican, went down the Río Tipuani, visited the mission of Guanai (the type locality of Calliandra inaequilatera), and then went up the Mapiri. In June of that year, he entered the Peruvian district of Caravaya and went down to Cuzco. Weddell met a Mr. Delondre in Cuzco and, after several days of pleasant but guarded conversation, discovered that he also was searching for Cinchona calisaya and, further, that he was a manufacturer of sulphate of quinine. Foreseeing difficulties with the government of Bolivia, Delondre had disassembled a factory for the manufacture of quinine and brought it by ship to the town of Valparaiso where he reassembled it. However, because of the strict limitations put on by the Bolivian government he was unable to obtain bark legally. He had contacted Pinto and Company, but they had sold their total output to a firm in New York for processing.

Weddell and Delondre collected in the valley of Santa Ana. They returned to the coast late in 1847, and Weddell went on to France. In Paris, Weddell's *Cinchona* seed lot was apparently divided, with some seeds being sent to England. The English sent their seeds on to Calcutta for growing, in an attempt to establish a quinine industry in India. After the seeds germinated in Paris the French turned over seedlings to the Dutch who, in turn, sent them directly to Java to start their plantations. The remaining seedlings were sent to Algeria. It seems to us quite possible that Weddell would have collected material other than that of

Cinchona and quite possibly could have collected the Calliandra because of its extraordinary beauty and potential use as an ornamental plant. This material could have gone the route from Bolivia to France to England to Calcutta to Java, or from Bolivia to France to Holland to Java. In either case the material could have reached Java, since the botanic garden there was coöperating with the one in Calcutta, and material was exchanged regularly. In addition, part of the Weddell seed collection apparently was turned over to a Parisian horticultural firm, since the Leiden Botanical Garden received a Cinchona calisaya via exchange with it in 1851. Seeds of ornamental species may have followed the same route. Leiden sent the Cinchona to Java where it arrived in 1852.

In 1849 Weddell published a classification of *Cinchona* based on his field studies. He was, as a result better qualified in 1851 when he returned to South America. In 1852, he entered the Bolivian *Cinchona* area and explored extensively. In the course of his travels he again passed through Guanai (the type locality of *Calliandra inaequilatera*). The results of this second expedition seem hardly to have been reported, but the seed distribution procedure may have been the same as that arranged at the end of the first one.

In 1852, the Dutch Minister of Colonies decided that a Cinchona growing area should be established in the colonies. He employed Justus Charles Hasskarl (1811–1894), a botanist who had been an assistant curator of gardens in Java for a period that ended in 1845. After receiving instructions in Holland, Hasskarl sailed from The Hague on December 4, 1852, charged "to collect plants and seeds of as many different species as possible." These instructions referred to species of Cinchona, but, since he was formerly associated with a botanic garden, it is unlikely that he would restrict his collecting to a single genus.

The expedition was publicized in a German newspaper, and, fearing that he would be unable to land in South America because of the publicity, Hasskarl sailed with a false passport under the name of José Carlos Müller. He landed in Lima and collected in Peru during the remainder of 1853 and the beginning of 1854. In March, 1854, he crossed the Andes to Puno "and after wandering over part of Bolivia," in April reached the village of Sina in the province of Caravaya near the frontier between Peru and Bolivia. It should be noted, in addition to his having wandered over "part of Bolivia," that Sina is only about 130 miles from Guanai, and it is quite conceivable that material of Calliandra could have been collected by him during this period. At this time Hasskarl, as José Carthrough an unscrupulous Bolivian agent. These were collected by a native near Ychu-corpa on the Bolivian frontier

Once he had the plants, Hasskarl took them to the Peruvian port of Islay, which is just north of the town of Mollendo. He had sent ahead word for help, and the Dutch warship *Prins Frederick Hendrik* met him Islay. The plants were placed in Wardian cases, and the ship set sail August 27, 1854. It was routed directly to Java and arrived December

13, 1854. It is widely reported that only two Cinchona plants survived, but a contradictory report indicates that there were 75. The latter number is probably correct.

On his return to Java Hasskarl was put in charge of the Cinchona cultivation project, and in connection with this he received additional Bolivian Cinchona seeds from Paris, presumably some of those collected by Weddell in 1852, and seeds of other species were sent from Peru. Seeds collected by Karsten in Colombia were received through the Governor of Curação. The significant point is that Hasskarl was indeed in Bolivia and in the general vicinity of the locality for Calliandra in 1854. His publication describing the newly cultivated Calliandra was in print by the end of the year of 1855. We think that the evidence, although highly circumstantial, indicates that Hasskarl may have collected the plants in Bolivia, have seen them flower aboard ship in Wardian cases, and at that time may have written his very extensive Latin description. This technique, i.e., description aboard ship, was well known to botanists of that era. Alternatively, it is possible that he did indeed obtain his material from Calcutta, and this, in turn, may have been received from the Weddell expeditions; or perhaps Hasskarl wished to cover his tracks in Bolivia and ascribed the plant to Calcutta without receiving seeds from there.

In 1860, the English botanist C. R. Markham was sent to Bolivia to collect additional material of *Cinchona*. He arrived on April 19th near the town of Crucero in the province of Caravaya and met there a Peruvian, Don Manuel Martel. Don Manuel "had a good deal to say, not very complimentary, about the Dutch agent who had come over to obtain Cinchona plants in 1854 for cultivation in Java." The bad feeling generated by Hasskarl affected Markham's expedition, and it was remarkable that he was able to bring his plants and seeds out of Bolivia safely. It should also be mentioned that the Bolivian agent with whom Müller-Hasskarl had dealt was forced to remove himself to another part of the country because of the threats and in fact, acts of physical violence by the local populace. It seems quite possible, then, that the material that was described either on shipboard or from cultivated material in Java was obtained through one of the tortuous routes described.

In postscript it should be mentioned that because of low yields none of the materials collected by these expeditions formed the basis for the rich Java Cinchona plantations. The honor of introducing a high-yielding strain fell to Charles Ledger or, perhaps more correctly, to his servant, Manuel Incra Mamani, who collected fourteen pounds of seeds of high-yielding Cinchona. One pound was sold to Holland for 100 francs plus £24 on germination. The remaining thirteen pounds of seed were partly sold on the streets of London, and the residue was purchased by a Mr. Money, of India, but on his return to India this lot failed to germinate. After all of the preceding efforts it seems ironical that the profitable Dutch Cinchona industry was founded on the purchase of a single pound of seed.

The history of the introduction of Calliandra inaequilatera into cultivation is almost as convoluted as that of Calliandra haematocephala but fortunately is better documented. Again the geographical focal point is the Bolivian town of Guanai. The first significant botanical event in the history of this Calliandra probably was a visit by Dr. H. H. Rusby, Dean of the College of Pharmacy of Columbia University, to Guanai in the course of his expedition of 1885-86. This particular expedition marked the beginning of Rusby's work in Bolivia. At the time he believed that he had arrived in Guanai approximately "three weeks too late," since the forest was primarily in fruit. This seems to be a curious situation, but he wrote that "the forest at that point consists almost wholly of mimoseae in prodigious variety." He said further that "the slope just back of the town was heavily forested, many of the trees being of really gigantic size. They belong chiefly in the senna, mimosa, and laurel families." In spite of the fact that most of the legumes apparently were in fruit, extensive collections were made, but most of these were lost in a boat mishap.

In 1889, Rusby hired Miguel Bang to collect herbarium material for him. Bang had been trained in gardening at Kew and had gone to Bolivia in 1883 expressly to collect living orchids to send to England. The enterprise failed, and Bang began collecting for Rusby. The herbarium material prepared by Bang was offered for sale from New York at \$10 per hundred specimens. Eventually this enterprise also failed, and Rusby was forced to suspend employment of Bang. The type material of Calliandra inaequilatera was collected by Bang in July, 1892, in the vicinity of Guanai. How large the individual gathering (Bang 1586) was, we do not know, except that six specimens have been reunited during this study. Apparently, no morphological information was included with the Bang collections, only a general locality and date. From this collection Rusby described Calliandra inaequilatera in 1896. The material was in flower only, and no fruit was seen.

The next important event was the Mulford Expedition for Biological Exploration of the Amazon Basin headed by Rusby (on his final Bolivian expedition). It was organized to make biological collections, field studies, and explorations on the eastern flanks of the Andes in Bolivia, Brazil, and Colombia. "The best equipped expedition ever to leave New York" concentrated early efforts on biological collecting in Bolivia. Among those accompanying Rusby was Dr. O. E. White, plant breeder from the Brooklyn Botanical Garden, who jointly represented the Brooklyn Botanical Garden and the Bussey Institution of Harvard University White, in addition to general collecting, obtained seeds of approximately 200 herbs, shrubs, and trees. The excursion began on June 1, 1921, as the group sailed from New York to Africa, Chile, and from there travelled by railroad to La Paz, Bolivia. From there the party proceeded by mule train and river travel in the general direction of the Amazon drainage. Collections were made along the Río Bopi, which drains into the Río Beni above the confluence of the Río Kaka. They established several

base camps, including ones at Huachi and Rurrenabaque; made extensive collections along the Río Beni, and at Rurrenabaque they had a temporary reunion with Miguel Bang.

We think that it was in the Río Bopi-Río Beni drainage that White collected seeds of Calliandra. Indirect evidence (see discussion of chromosome numbers) points to the origin as "Huachi" (San Miguel de Huachi). Because of illness Rusby was forced to leave for New York in December, leaving White in charge of the faltering expedition. White continued collecting until March 15, when the expedition disintegrated, from the biological point of view, and he and some of his companions left for New York, via the Amazon River. Shortly after White's return on April 14, 1922, the dried specimens were sent to Rusby at the New York Botanical Garden, while White took the seeds to the Brooklyn Botanical Garden. Eleven years later the Brooklyn Botanical Garden exhibited a vase of flowering C. inaequilatera at the January 20th meeting of the Horticultural Society of New York and won an Award of Merit for the entry. One of the plants from the original seed lot, now a repeatedly pruned tree with a trunk eighteen inches in diameter, is still growing in the Brooklyn collection.

According to Hayward (1955), the first record of the shrub's introduction into Florida was three plants of *Calliandra inaequilatera* that were sent in 1933 to Dr. George Tyrell, a horticulturist at LaBelle, Florida. He, in turn, gave stock to Dr. E. A. Menninger, who is responsible for its wide distribution and status as a desirable ornamental for tropical climates. The primary method of propagation of the plant is by the seed (Menninger, *in litt.*), although the progeny are variable and not reliable. The plants seem to be quite variable in regard to the number of fruits set, and some plants seldom fruit. The principal hortitural selections have been made on the basis of the color of the staminal filaments, the most conspicuous parts of the showy heads of flowers.

Recently (1963), Cowan in reviewing the taxonomy of the cultivated powder-puff trees concluded that two species, Calliandra haematocephala and C. inaequilatera are being grown. He presented keys, descriptions, and discussion of each species. His maintenance of the two as distinct species was based, not on opposing qualitative characters, but on variations of the same quantitative characters, usually with considerable overlapping. We have carefully re-examined the vegetative characters, including petiole length, terminal leaflet size, and degree of leaflet pubescence, which supposedly were useful in distinguishing the two species. The petioles of C. haematocephala were reported to be 10-20(-25) mm. long, while those of C. inaequilatera were (15-)25-40(-50) mm. long. In addition, his study indicated that the median and terminal leaflets of C. haematocephala are smaller, [20-]23-47 mm. long by [5-]7-17 mm. broad, and more numerous than those of C. inaequilatera, which are [45-] 50-75 mm. long by [15-]20-30 mm. broad. Our own study shows that petiole length, a highly variable character, is independent of leaflet size

and number, with both short to long petioles being found on specimens attributed to each of the two "species" in question.

Although selected elements of Old World cultivated "populations" of C. haematocephala can be separated on the basis of leaflet size from similar selected elements of C. inaequilatera, there is complete gradation between the two on this character. Indeed, many specimens have intermediate leaflet sizes. Examination of living plants substantiated the unreliability of this character, for leaves with small leaflets can be found on the same branch with leaves with large leaflets (see Figure 2). The Old World specimens typically have the leaves glabrate and ciliolate, whereas New World ones have varying amounts of leaflet pubescence. We suspect that this is due primarily to a more restricted genotype in the Old World material, probably because of a smaller original sample size. An examination of the holotype and five isotypes of C. inaequilatera showed considerable variation in the degree of pubescence of the leaflets.

The floral characters, corolla-lobe size and position in age, length of the



FIGURE 2. Outlines of four leaves from a single vegetative branch of Calliandra haematocephala showing size variation.

corolla tube, and peduncle length were also examined and found to be unreliable in distinguishing the two "elements." Although a longer peduncle length is usually found in plants with smaller and narrower leaflets, no clear separation could be made, for the peduncular lengths of Calliandra haematocephala overlap with those of C. inaequilatera. Likewise, the longer lanceolate corolla lobes attributed to C. haematocephala, as well as shorter, more ovate ones, could be found on specimens of C. inaequilatera. The length of the corolla tube, like the other characters examined, showed a continuous gradation from 3 to 7 mm. The position of the corolla lobes, erect versus reflexed, could not be adequately assessed. This condition does not appear to be genetically controlled. Some of the lobes becoming reflexed may result from the pressing techniques of the collector. In sum, the taxonomic characteristics of the flowers, as well as those of the vegetative parts, fail to differentiate two taxa after a careful analysis of a sizable sample of specimens, both wild and cultivated.

The unreliability of the characters previously used to distinguish the two "species" of *Calliandra* is not in itself sufficient reason to treat them as a single species because of the peculiar circumstances that led to the plant's being known to science in cultivation prior to its being known to science in nature. In the following paragraphs we point out a few peculiar morphological features which link the specimens into a single species and when considered in conjunction with the historical aspects serve to confirm further the morphological conclusions. On the totality of these considerations we believe that there is no justification for recognition of more than one species, the correct name of which is *C. haematocephala* Hasskarl.

The most unique floral feature of Calliandra haematocephala is the structure of the androecium. As in all species of the genus, the stamens are basally connate into a staminal tube of varying length. In C. haematocephala the tube generally equals or exceeds the corolla lobes (see Fig-URE 3.) An irregular number of small fimbriae are inserted at the mouth of the staminal tube. These fimbriae, which have been referred to in previous literature as a "quasi corona," are irregular in both size and shape (generally not more than 1 mm. in length) and often erose at their apices. They are derived from staminal tissue at the orifice of the filament tube, and they may either represent aborted stamens or be irregular enations that are not vascularized. The fimbriae are oriented with their apices directed towards the center of the staminal tube orifice and form a somewhat dome-shaped structure covering it in functionally staminate flowers or permitting only the style to pass in bisexual flowers. They are white, as is the staminal tube, in stark contrast to the variously redhued filaments. That such an abrupt color change occurs at the filament tube orifice implies more than casual biological significance. This significance probably can be determined properly only in field studies.

It has been long recognized that in *Calliandra*, as in many other genera of the Mimosoideae, the pollen is found in "massulae," or clumps. In *Calliandra* two types of "massulae" are found: a sixteen-grained, disc-like polyad

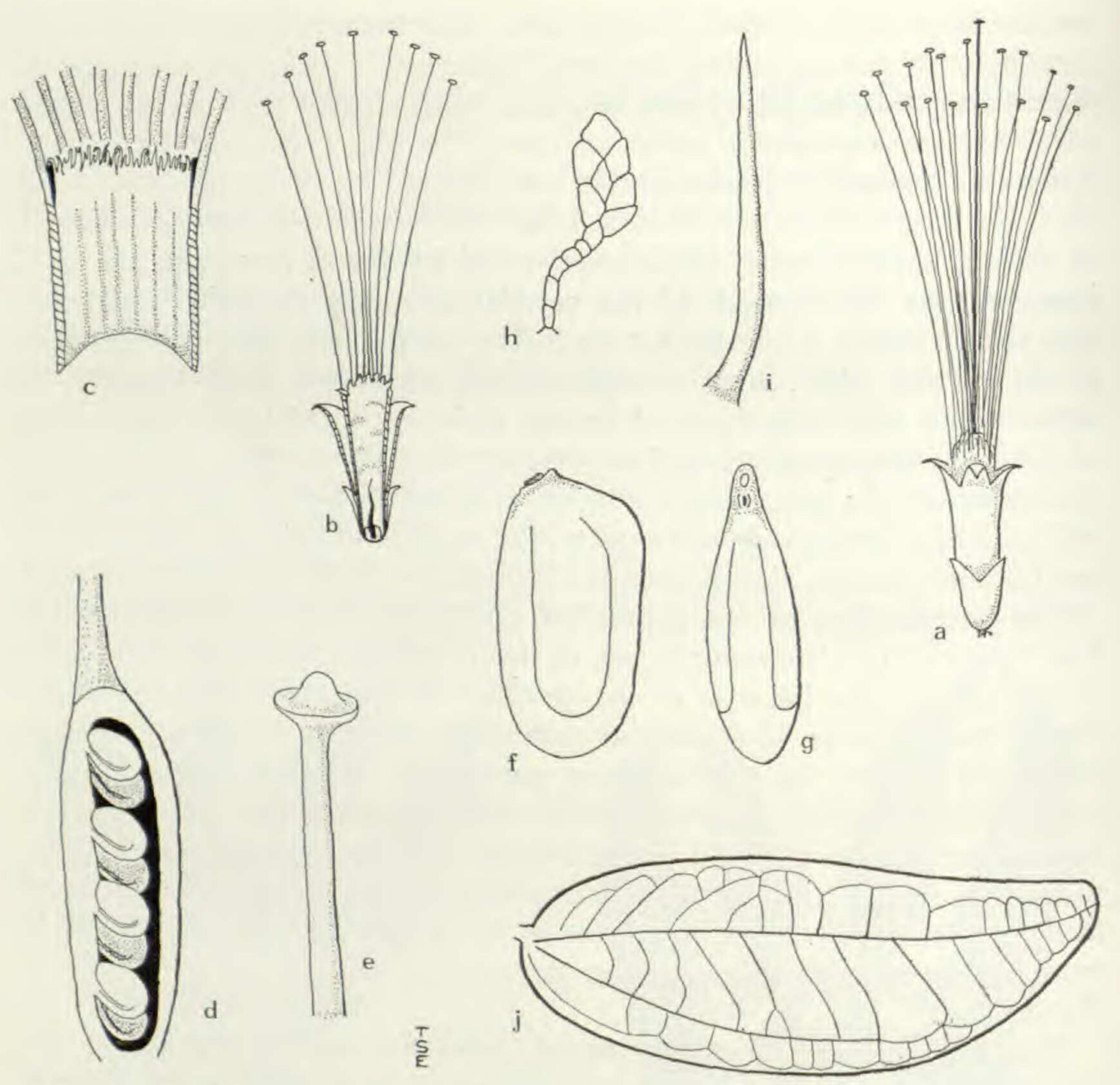


Figure 3. Calliandra haematocephala: a, bisexual flower, × 1.5; b, longitudinal section of functionally staminate flower, × 1.5; c, longitudinal section and internal view of upper portion of filament tube showing fimbriae, × 5; d, longitudinal section of ovary, × 45; e, portion of upper style and stigma, × 45; f, lateral view of seed showing pronounced U-shaped pleurogram, × 5; g, face trichome, × 215; i, unicellular trichome, × 215; j, mature leaflet with prominent venation, × 2.

and an eight-grained, flattened ellipsoidal polyad. The polyad of *C. haematocephala* is of the latter type (Figure 4). Although it has been figured in both systematic (Kunth, Mimos. Pl. Légum. 70–73, *t.* 22. 1820) and palynological texts (G. Erdtman, Handbook of Palynology, Munksgaard. 378, 379. 1969) its taxonomic and biological significance has never been realized. The morphology and orientation of the "massulae" is of extreme importance in determining the biological significance of this polyad. In *C. haematocephala* the staminal filaments are erect at anthesis and form on the back in a median position at right angles to the axis of the filaments. Thus the "face" of the anther is directed away from the center

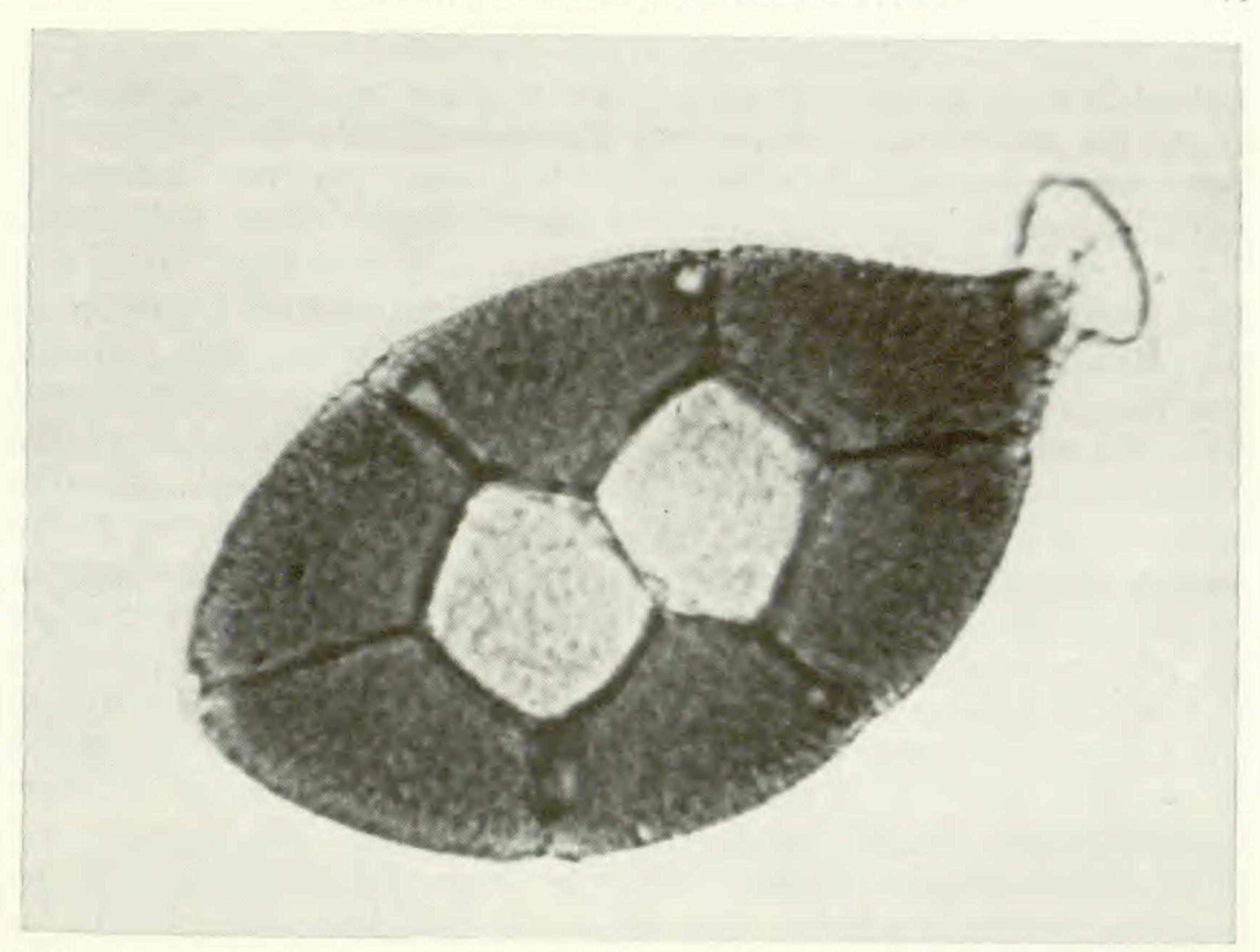


FIGURE 4. Photomicrograph of fresh polyad of Calliandra haematocephala stained with aniline blue in lactophenol. The adhesive droplet in upper right-hand quadrat distorted from normal spherical shape because of attachment to microscope slide. Actual length of polyad ca. 160 μ .

of the inflorescence. Flowering proceeds from the base of the inflorescence to the apex but the process is so rapid that, for practical purposes, it may be considered synchronous. As soon as the filament straightens, the anther begins to open by two longitudinal slits. Within each of the four anther locules lie two yellow eight-grained polyads. Each flattened polyad is composed of two median pollen grains and six peripheral ones. One of the peripheral grains is modified slightly and has a somewhat eccentric and pronounced projection. This special grain, the foot grain, lies at the proximal end of each polyad and the two foot grains of the polyad pair are directed toward one another. All previous published illustrations of the eight-grained Calliandra polyad show this detail but not the orientation within the anther. The significant point that has not been mentioned is that between the apices of the "foot grains" an extremely viscous substance (that cannot be seen in acetylized material) is formed. As the anther opens the polyads are not only exposed, but the polyad pairs are separated, and their sticky apices are rotated until they are directed away from the anther by at least 90 degrees. The polyad bases are held in the old locules. The mechanism of this maneuver is not known, but it may be related to a rather large disc-like structure on the back of the anther that surrounds the filament. At anthesis the polyads are held with their apices directed outwards, and each apex is covered by a glistening drop of ad-

hesive material. Analogy to the pollinia of Asclepiadaceae and Orchidaceae is irresistible. In an inflorescence of some forty flowers (which seems to be an average number in an inflorescence of a well-grown C. haematocephala) there may be approximately 25 anthers per flower (varying between 20 and 30), making approximately 8000 polyads available for pollination. This number coupled with the polyad orientation presents a formidable mechanism for any pollinator to avoid. Unfortunately, we do not know the pollinator, but on the basis of inflorescence position, filament color, and direct observation of other species, one suspects humming birds (and if so, this would account for the restriction of this type of polyad to the New World species of Calliandra and would thoroughly substantiate the opinion that the original plants of C. haematocephala were of New World origin). The slightest contact with the adhesive drop of the polyad causes the polyad to be transferred to the vector, as can easily be demonstrated in the laboratory with a needle or glass slide. About midway through the first day of anthesis the stigmatic surface is at a level with the anthers and becomes glistening and quite sticky. Polyads touched to the stigma at this time easily break their original attachment and become adherent to the stigmatic surface. By the second day of anthesis the stigma seems to be somewhat less receptive, and stylar elongation has elevated it beyond the horizon of anthers. The wilting of individual flowers begins towards the end of the second day and usually is completed early in the third day.

Individual inflorescences vary in the total number of flowers and in their functional capabilities. The androecium is functional in all flowers, but varying numbers have the gynoecium aborted. The result is that bisexual and functionally staminate flowers are found in most inflorescences, and the ratio of polyads to stigmatic surfaces is therefore greatly increased. In Calliandra haematocephala we have found a general tendency for the bisexual flowers to be clustered towards the center of the inflorescence (individual inflorescences thus assuming the functional role in pollination of an individual flower). In a few instances the entire inflorescence was composed of functionally staminate flowers. In other species of Calliandra the tendency towards dimorphism is developed to the extent of producing truly dimorphic flowers. A further development in the efficiency of the reproductive cycle is found in the ovary of the bisexual flowers, which has only eight ovules. Thus the transfer and proper germination of a single polyad could assure fertilization of all available ovules. In sum, the reproductive cycle in Calliandra haematocephala appears to be highly specialized with a high correlation of ovule number with polyad pollen

A detailed account of micro- and megasporogensis (lacking any mention of the pollination mechanism) has been presented by Dnyansagar (1958). He concluded that the eight-grained polyad of Calliandra haematocephala is composed of two isobilateral tetrads. The individual pollen grains are binucleate according to Dnyansagar but Brewbaker (1967) has reported them to be trinucleate (in C. inaequilatera). Most likely one of

these reports is incorrect as a result of misidentification of the specimen. There are two chromosome number reports for Calliandra haematocephala, both made by Earlene Atchison from mitotic divisions. The first count, 2n = 16, was made from material grown at the Blandy Experimental Farm from Huachi, Bolivia (Jour. Elisha Mitchell Soc. 65: 118–122. 1949). This count is based on the O. E. White material and provides the only precise information on the origin of the material introduced at Brooklyn. We believe this locality information came directly from Dr. White to Dr. Atchison. The second count, 2n = 16, was made from material grown at the Atkins Garden, Cuba (Am. Jour. Bot. 38: 538–546. 1951). An examination of the voucher specimen, Atchison 91 (GH), shows that it is not C. haematocephala but another species of the genus. The only other chromosome count reported for the genus is that for C. pittieri, which has 2n = 32 (Jour. Agri. Sci. Tokyo Nogyo Daigaku 8: 49–62. 1962).

Calliandra haematocephala Hasskarl, Retzia 1: 216-219. 1855.

Calliandra inaequilatera Rusby, Mem. Torrey Bot. Club 6: 28, 29. 1896.

Anneslia haematocephala (Hasskarl) Britton & Wilson, Sci. Survey Porto Rico & Virgin Islands 6: 348. 1926.

Shrubs or small trees to 5 m. high, frequently spreading and forming a ± rounded crown; branches and branchlets terete, the latter with numerous inconspicuous lenticels, glabrate to densely puberulent, with minute multicellular glandular trichomes on most vegetative parts; conspicuous short shoots often present. Leaves alternate, bipinnate, eglandular, with one pair of pinnae, petiolate; petioles canaliculate, 0.7-3.25(-4.75) cm. long, slightly swollen at the base, sparingly puberulent to densely pilose, with a small apiculum between the insertion of the pinnae; rhachides 4.5-11.5 (-15) cm. long, canaliculate, sparsely to densely pilose, terminated by a small lanceolate apiculum; pinnae with (4-)5-8(-10) pairs of leaflets; the basal pair of leaflets reduced, subopposite, the inner leaflets smaller, the terminal leaflets narrowly ovate, elliptic, to obovate, 1.5-8.4 cm. long, 0.5-3.5 cm. broad, \pm falcate, oblique and rounded at the base, obtuse to acute and mucronulate at the apex, glabrate to pilose, generally ciliolate, with 3 primary veins (2 prominent and 1 subprominent) palmately arranged, chartaceous; stipules ovate to infrequently lanceolate, 2-10 mm. long, 1-3 mm. broad at the base, acute at the apex, persistent, often crowded on the short shoots. Inflorescences capitate, 20-45-flowered, borne singly or in pairs in the leaf axils, pedunculate, the peduncles erect, 1.2-3.3 (-5.3) cm. long, pilose, often densely so. Flowers bisexual or functionally staminate by gynoecial abortion, 5-merous, pseudo-actinomorphic, sessile, bracteate, the bracts elliptic, to 1.5 mm. long, striate and ciliolate. Calyx tubular to subcampanulate, 1.5-3 mm. long, striate and sparsely puberulous to glabrate, greenish, the lobes ovate, 0.5-1 mm. long, obtuse at the apex, ciliolate, erect, aestivation valvate. Corolla tubular and flaring slightly towards the orifice, 3.5-8 mm. long, glabrous or with

a few unicellular trichomes interspersed with minute, multicellular, glandular trichomes, reddish, the lobes lanceolate, 2-3 mm. long, ca. 1.5 mm. broad at the base, sparsely ciliolate, usually erect at anthesis, aestivation valvate. Stamens ca. 25, basally connate into a staminal tube, the tube usually equalling or often surpassing the corolla lobes, with numerous irregularly shaped fimbriae, to 1.5 mm. long, inserted within the orifice and forming a dome-like structure at the tube apex, the filaments becoming free at various levels, filiform, 3-4 cm. long, white at base to various intensities of red towards apex; anthers oblong, attached on the back, with a disc-like structure surrounding filament at the point of attachment, dehiscing by longitudinal slits directed away from base of flower; pollen united into 8-grained polyads, the polyads elliptic and flattened, 160 μ long, and ca. 88 µ broad, with one grain eccentric and bearing a drop of adhesive material, each anther bearing 8 polyads. Disc cupuliform, 0.5-0.75 mm. tall, fleshy, glabrous. Gynoecium 1-carpellate, the ovary tetragonal, 3-4 mm. long, glabrous, the style filiform, 3-4 cm. long, red, glabrous, the stigma dome-shaped, ca. 0.5 mm. in diameter, adhesive at anthesis; ovules anatropous, 8; in functionally staminate flowers the aborted gynoecium of various sizes. Legume elastically dehiscent, linearoblanceolate, 8-12 cm. long, 1-1.5 cm. broad, with a broad valve and narrow but conspicuous margins, brown, usually 5-6-seeded, the seeds oblong, flattened laterally, 0.8-1.2 cm. long, 0.4-0.6 cm. broad, each side marked with a conspicuous pleurogram, hilum eccentric.

SPECIMENS EXAMINED (SPONTANEOUS):

Bolivia. La Paz: vicinity of Guanai, July 1892, Bang 1586 (holotype NY; isotypes A, GH, MO, NY); Ixiamas, Dec. 15, 1921, Cardenas 2011 (BKL, GH); Isapuri (on Río Kaka) Oct. 5, 1901, R. S. Williams 725 (K, NY, US). SANTA CRUZ: Buena Vista, April 1–26, 1921, Steinbach 5612 (A, GH), June 26, 1925, Steinbach 7154 (A, GH); Santa Cruz, May 1892, Kuntze s.n. (US), June 1892, Kuntze s.n. (NY), July 2, 1968, H. Adolfo M. (US); between Puerto Chuelo and Buena Vista, Mar. 14, 1964, Badcock 10 (K).

SPECIMENS EXAMINED (CULTIVATED):

United States. Connecticut: Danielson, Logee's Greenhouses, July 1969, Gibson 1246 (AAH). New York: Brooklyn Botanic Garden, Mar. 1932, Everett s.n. (BH-2 sheets), Mar. 1970, McGourty (origin, Bolivia) (AAH), New York Botanical Garden, Nov. 1955 (NY). Pennsylvania: Kennett Square, Longwood Gardens, Dec. 1955, Huttleston 1203 (AAH, GH, NA), Jan. 1961, Huttleston 1838 (origin, Edinburgh Bot. Gard.) (AAH, BH), Jan. 1961, Huttleston 1839 (origin, Florida) (BH), Jan. 1961, Huttleston 1841 (origin São Paulo, Brazil) (BH), Jan. 1963, Peele 1008 (origin, Atkins Garden, Cuba) (BH), Jan. 1964, Peele 1254 (BH), Jan. 1964, Huttleston 2021 (origin, Atkins Garden, Cuba) (NA). Florida: Fairchild Tropical Garden, Dec. 1959, Howard 14929 (AAH), Feb. 1969, Gillis Naples, Caribbean Gardens, Feb. 1967, Cooley & Brumbach 11815 (AAH); Oneco, Reasoner Bros. Nursery, Jan. 1932, T. R. Robinson s.n. (NA); Oneco, Royal Palm Nurseries, Jan. 1932 (BH), Apr. 1932 (BH); Tampa, Mar. 1956, Reese 942

(GH, NA); Winter Haven, Dec. 1964, Mazzeo 846 (NA), Dec. 1967, Mazzeo 2419 (NA); Winter Haven, Cypress Gardens, Jan. 1968, Mazzeo 2468 & 2473 (NA); Winter Park, Lakemont Gardens, Feb. 1956, Wyndham Hayward (K). Texas: Houston, Dec. 1945, E. Teas s.n. (CAS). California: Azusa, Monrovia Nursery, Nov. 1960, McClintock s.n. (CAS); University of California campus, Mar. 1964, McClintock s.n. (BH, CAS); La Jolla, garden, Mar. 1956, McNeill s.n. (CAS); West Los Angeles, Vavra Estate, Jan. 1959, Raven, Turner & Whitesel C103 (CAS); Santa Barbara, Harvey Estate, Jan. 1957, C. Smith s.n. (CAS); Santa Barbara, Hillside Park, Dec. 1956, McClintock s.n. (BH, CAS); Santa Monica, Evans and Reeves Nurseries, Nov. 1942, McClintock s.n. (BH).

Bermuda. Paget, Botanical Gardens, Nov. 1963, Manuel 120 (AAH). Dominican Republic. Santiago City, May 1956, Jimenéz s.n. (US). Puerto Rico. Agricultural Experiment Station, Feb. 1921, Hume 2146 (NA); Hato Rey, Pennock Garden, Feb. 1967, Howard 16321 (US), 16339 (AAH); Km. 22 on Route 191 through Luquillo Mts., Jan. 1965, Wagner 741 (AAH). Curação. Museum Garden, Dec.

1959, Fr. M. Arnoldo 2257 (US).

Ecuador. Hda. Angelica, Chobo, Aug. 1921, Popenoe 1351 (US). British Guiana. Georgetown, Botanic Gardens, Feb.-Mar. 1922, Bailey 566 (BH). Brazil. Rio de Janeiro, Jardim Botanico, Dec. 1928, Ducke 16078 (US); São Paulo, Parque

Instituto Agronomico, Apr. 1938, Santoro 1574 (us).

India. Lucknow, National Botanic Gardens, Dec. 1966, Sharma 68601 (AAH); Dehra Dun, 1928, Singh 80 (AAH); Bally gunge, Calcutta, Nov. 1877, Gamble 5792A (K). Singapore. Botanic Garden, Oct. 1924 (BH), 1929, Clemens & Clemens 22525 (AAH). Java. Buitenzorg, Botanic Garden, Hasskarl s.n. (AAH, fragment of type material); 1903 (US), Oct. 1903, Sargent s.n. (AAH).

Philippines. Luzon: Los Baños, Feb. 1954, Steiner 493 (us); College of Agriculture Campus, Nov. 1946, Sulit PNH 7022 (AAH), Sept. 1949, Sulit PNH 9350 (AAH), Dec. 1949, Sulit PNH 12189 (AAH), Mar. 1958, MacDaniels 21 (BH).

United States. Hawaii: Honolulu, Old Pali Rd., Aug. 1961, McClintock s.n. (cas).

England. Royal Botanic Garden, Kew, Mar. 1959, E.N. 211/45 (origin, Peru) (κ), Feb. 1938, E.N. 581/32 (origin, Brooklyn Botanic Garden) (κ), Jan. 1966, E.N. 211/45 (κ), Jan. 1966, E.N. 342/56 (origin, U.S. Dept. Agriculture) (κ). France. Les Cèdres, St. Jean, Cap-Ferrat, Jan. 1963, Marnier-Lapostolle (κ) (white-flowered form).

South Africa. Pretoria, Botanic Gardens, Aug. 1967, Mills 84 (AAH).

Perhaps the impression has been given that because all the cultivated material known as Calliandra haematocephala and C. inaequilatera must be considered as a single species (and the name Calliandra haematocephala applies) that no taxonomic problems remain. This is not the case as there seems to be greater difficulty in determining the range of variation of the species in the wild than that encountered in collating the cultivated with the wild material. In this connection several populations of Calliandra must be considered. The first and the most perplexing, is a population that occurs at Guanai and Mapiri. The Mapiri population is represented by Rusby 1315 (NY) and the Guanai population represented by Rusby 1314 (NY) and Bang 1603 (A, GH). As the basis for his Calliandra boliviana Britton used the Rusby collections which were made in May, 1886 and which must have been among the specimens not lost in the river. There is no question that the material above belongs to this complex. The

question is whether or not C. boliviana should be a synonym of C. haematocephala. The flowers are almost identical with those of C. haematocephala, except for a very slight difference in the lobing of the calyx. The leaves have far fewer leaflets, and each individual leaflet is much larger than the leaflets found in the collections of C. haematocephala. The problem seems to be whether or not these represent two ecological types, i.e., whether or not they are ecologically separate but geographically sympatric species.

A second population of Calliandra boliviana occurs in the basin of the Río Bopi in the department of La Paz. This population is represented by Krukoff 10220a (A), Rusby 654 (BKL, GH), and White 443 (BKL, GH, K). Unfortunately, none of this material is in flower, so no direct comparisons can be made. The leaves tend to be similar to the Guanai-Mapiri population of C. boliviana, except perhaps the even fewer and larger leaflets. Calliandra boliviana has been placed in the synonymy of C. bombycina Benth., an action that appears to be totally unjustified. Calliandra bombycina seems to be restricted to the Río Huallaga drainage in the province of San Martín, Peru. The flowers lack fimbriae at the orifice of the staminal tube.

A very interesting population of Calliandra haematocephala grows at the town of Buena Vista in the department of Santa Cruz. This population is typified by somewhat smaller flowers than those of the type material of Calliandra inaequilatera, and the staminal tube is exserted only slightly and not several millimeters beyond the corolla lobes as one finds in all the Guanai material. There appear to be two leaf sizes present in these collections, probably on different branches, on one of which the leaflets are medium-sized, and on another of which the leaflets are very much reduced in size. In both cases the leaflets are densely pubescent. Steinbach's notes indicate that the plants occur both in the forest and in the pampas region. It is possible that these plants represent a separate but very closely related species, but we have chosen to treat them as C. haema-

We are indebted to the directors and curators of those institutions which graciously loaned materials for study. These include:

- Arnold Arboretum, Harvard University, Cambridge
- Arnold Arboretum, Harvard University, Jamaica Plain BH
- Bailey Hortorium, Cornell University, Ithaca
- Brooklyn Botanic Garden, Brooklyn
- California Academy of Sciences, San Francisco Gray Herbarium, Harvard University, Cambridge
- Royal Botanic Gardens, Kew K
- Missouri Botanical Garden, St. Louis MO NA
- United States National Arboretum, Washington NY
- New York Botanical Garden, Bronx US
- U.S. National Museum, Smithsonian Institution, Washington

A number of individuals have assisted us in a variety of ways, and we are grateful for their help. Among these are Mr. Russell Edwards, of

the Blandy Experimental Farm; Dr. Patricia Holmgren, of the New York Botanical Garden; Dr. Donald G. Huttleston, of Longwood Gardens; Dr. E. Milne-Redhead, of Kew; Dr. Frederick McGourty, Jr., of the Brooklyn Botanic Garden; Dr. Edwin A. Menninger, of Stuart, Florida; Dr. S. N. Mitra, of the Botanical Survey of India; Dr. Howard Pfeifer, of the University of Connecticut; and Dr. C. G. G. J. van Steenis, of the Rijksherbarium, Leiden. We are much indebted to our colleagues and students of the Arnold Arboretum and Gray Herbarium for extended discussion and suggestions which led to the final manuscript.

BIBLIOGRAPHY

Anonymous. Calliandra haematocephala Bot. Mag. 86: t. 5181. 1860.

Boerlage, J. G. Justus Karl Hasskarl en zijn botanische werken. Teysmannia 5: 129-148. 1894.

Brewbaker, J. L. The distribution and phylogenetic significance of binucleate and trinucleate pollen grains in the angiosperms. Am. Jour. Bot. 54: 1069-1083. 1967.

Cowan, R. A. Correct name of the powder-puff tree. Baileya 11: 94-98. 1963. Dnyansagar, V. R. Embryological studies in the Leguminosae. VIII. Acacia auriculae formis A. Cunn., Adenanthera pavonina Linn., Calliandra haematocephala Hassk., and Calliandra grandiflora Benth. Lloydia 21: 1-25. 1958.

DURAN-REYNOLS, M. L. The Feverbark Tree. Doubleday. 1946.

HAYWARD, W. Calliandra, what kept you? Tropical Homes and Gardens 6(1): 27, 39. 1955.

Lowis, L. Familiar Indian Flowers. t. 7. 1878. [C. haematocephala as "Calistemon Linearis."]

MacCreagh, G. White Waters and Black. Century Co., New York and London, p. 404. 1926.

Markham, A. H. The life of Sir Clements R. Markham. John Murray, London, p. 384. 1917.

MARKHAM, C. R. Peruvian Bark. London, p. 550. 1880.

Mason, H. Try your hand at Calliandras. Tropical Homemaker and Gardener. 7(1): 16. 1956.

Club 3: 1-67. 1893.

TAYLOR, N. Cinchona in Java. Greenberg, New York. p. 388. 1933.

Weddell, H. A. Voyage dans Le Nord de La Bolivie. Paris, p. 571. 1853.

WHITE, O. E. Botanical Exploration in Bolivia. Brooklyn Bot. Gard. Rec. 11: 93-105. 1922.

ARNOLD ARBORETUM AND GRAY HERBARIUM
HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138
AND

ARNOLD ARBORETUM

HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS 02138